Movement ecology of ungulate communities

– effect of species densities and habitat selection

Rörelseekologi i klövviltssamhällen - effekten av artdensitet och habitatval

Linda Zetterkvist

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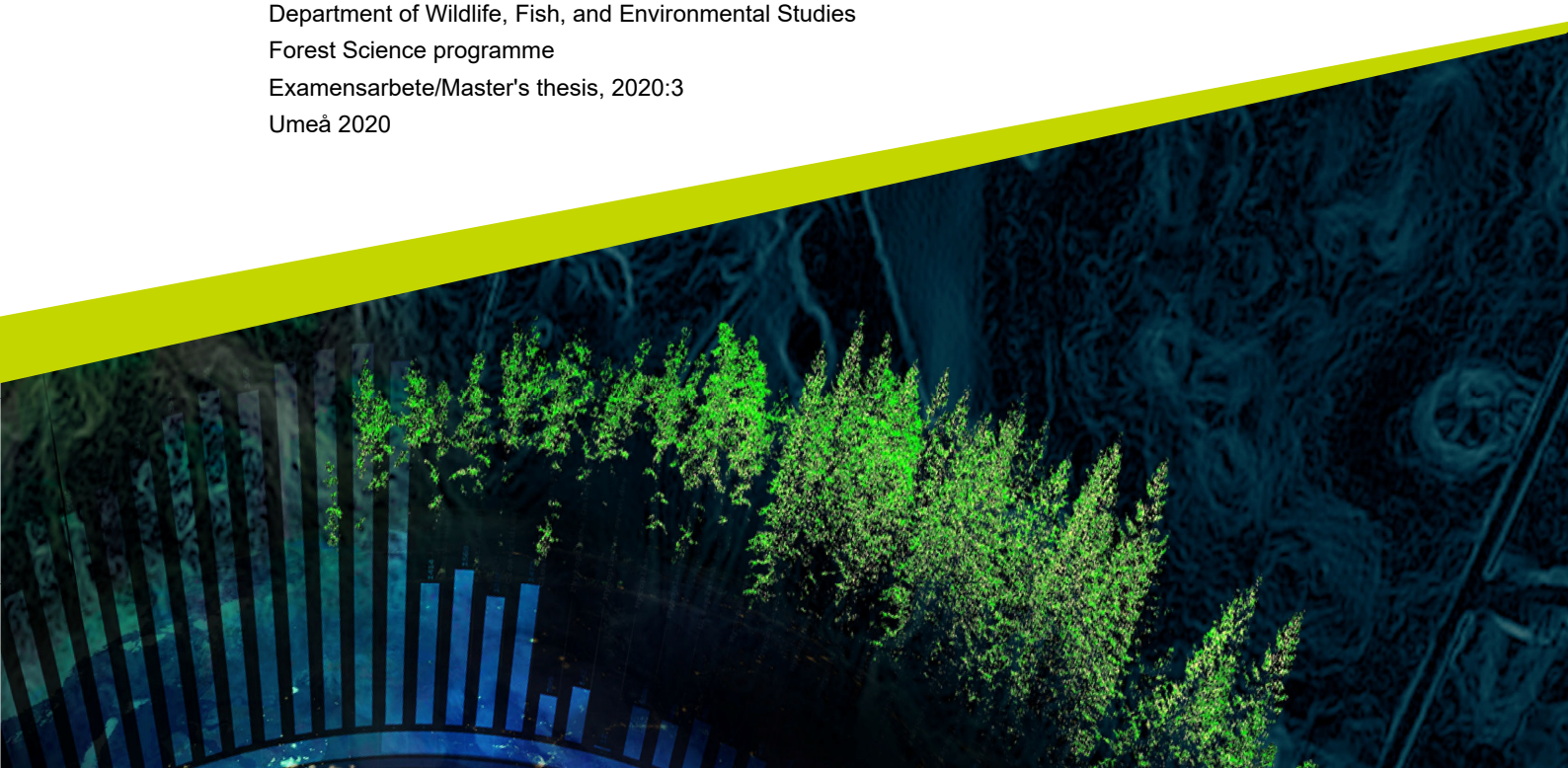

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Abstract

Animal movement is a topic important in various different ecological perspectives. Ungulate species are an important source of income, hunting game and subject for protection and management all across the globe. As multi-species management is becoming more common- information about movement patterns in relation to other ungulates and habitat selection may help to improve this matter. With data derived from moose (*Alces alces*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), all located in a Swedish Nordic peninsula called Järnäshalvön, I chose to investigate this further.

In this study I used telemetry data derived from GPS-collars on all three species to fit step-selection functions (iSSF) to habitat- and ungulate density covariates. Habitat covariates were retrieved from the Swedish land surveying agency in the form of a land use raster over the study area. Density covariates were created from pellet count- and camera trap data for each of the study species. All three species selected for clear-cut areas rather than forested areas during autumn and summer. Moose and red deer selected clear-cut areas during all four seasons which highlights the importance of directed management in order to prevent potential browsing damages on young forest stands. Differences in diurnal habitat selection were also visible where red deer stood out and selected for the majority of the habitat types during night, except for during summer. Moose and roe deer selected for low/medium densities of each other whilst red deer avoided low densities of roe deer. These results show that habitat selection differs amongst these three sympatric species and is also affected by season of the year and time of day. Densities of other ungulates clearly affects movement patterns, however, the resolution of the density covariates in relation to the telemetry data led to some limitations with the use of iSSF to generate results.

Keywords: Step-selection, wildlife management, diurnal activity, moose (Alces alces), red deer (Cervus elaphus), roe deer (Capreolus capreolus)

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1. Introduction

Movement ecology has for a long time been interesting from various ecological perspectives as well as wildlife management (Allen & eSingh 2016; Benson 2016). With humans introducing new species all over the planet the impact of species movements, interactions and abundances is now, more than ever, a subject for wildlife management.
The presence and distribution of different ungulates in Sweden has been changing through history, where moose (*Alces alces*) has been the most dominating species across the majority of the country, and still is (Jarnemo et al. 2018), however, now sharing the space with sometimes multiple other ungulates. Through time humans has been introducing new species, as well as facilitating species like roe deer (*Capreolus capreolus*) to spread north due to favorable habitat alterations and milder climate and now they occur all the way to the tree line (Jarnemo et al. 2018.). Similarly, red deer (*Cervus elaphus*) is also spreading north with the help from humans (Jarnemo et al. 2018), which now has led to these three species coexisting further across the country. Multi-species ungulate communities are a rising problem Sweden is starting to feel the impact of in the form of browsing damages on coniferous young forest and crops (Spitzer 2019; Nichols & Spong 2014). Multi-species management is therefore becoming more and more important. As these species compete for the same or similar resources, the importance of knowledge about species interactions is ever more crucial (Spitzer 2019).

With increased knowledge on how these three ungulate species interact together, regarding habitat selection and movement patterns in relation to one another, species management and potential forest damages could become easier to predict and prevent. In a study by Prokopenko et al. (2017) they demonstrated how animal movement can be linked to habitat features, in this case roads, to investigate how elk respond to this landscape feature.

Moose is known to browse on young pine stands during winter (van Beest et al. 2010; Spitzer 2019) causing losses in forest growth, however, its preferred choice of food is rowan, aspen and sallow (Wam et al. 2010), especially during summer months. During spring and autumn, lingonberry (Vaccinium vitis-idaea) and bilberry (Vaccinium myrtillus) is an important source of food. This means that

moose adapts its forage depending on seasonal changes and therefore its habitat selection. Young forest stands less than four meters in height are mostly preferred as forage for moose (Bergqvist et al. 2018) and with today's modern forestry these types of young forest stands are now a common sight in the Swedish landscape, providing the moose with plenty of forage (Speed et al. 2013). However, potential competition from introduced species may influence the moose choice of forage and movement patterns and indirectly also the extent of potential forest damages. Spitzer (2019) concluded that moose consumed more pine in areas with high deer density rather than Vaccinium spp., high snow depths also lead to moose increasing their brows on pine but did not affect consumption of Vaccinium spp. However, foraging on Vaccinium spp. was highest in August when deer density was high and coincided with lowest consumption for the other smaller deer species.

In contrast to moose, roe deer is known for its demand of food of high-quality, being a browser (Spitzer 2019), adapting its forage over the seasons to find the best forage (Moser et al. 2006). As for moose, roe deer preferably use clear-cut areas for forage and cover (Vospernik & Reimoser, 2008; Putman 1996) due to the high amount of high-quality food consisting of young sprouts and shrubs. Vaccinium spp. is an important source of food for roe deer during especially spring (Mach-April). Spitzer (2019) found that roe deer increased their consumption when deer densities was high. During winter, home-range size increase for both sexes as a response to tougher conditions finding good forage. However, in northern Sweden, high snow depth decreases roe deer's ability to move long distances in search for food and therefore restricts them to smaller areas where minimal snow depth and good movement ability is important (Ossi et al. 2010)

Red deer, as a mixed feeder, forage on various different types of plants, herbs and shrubs, and like roe deer, it prefers high-quality food (Spitzer 2019, Putman 1996). During summer red deer preferably use wet and dry mires if available and during winter and autumn, coniferous stands were most frequently used (Putman 1996). Red deer is known for its habit of stripping bark of trees where coniferous trees seems most desired. This is a common problem for forest owners with red deer present. In a study by Borkowski & Ukalski (2011) they argue that bark stripping increased when cover conditions from understory trees was low as well as low tree height. When comparing elk in Canada and red deer in the Netherlands, Ensing et al. (2014) saw a difference in activity depending on time of day, elks were more active during the day, while red deer were most active during the night. This was suggested to be as a response to human disturbances as well as local weather.

Movement behavior differs amongst the three species as well as differing food requirements, body size and life history strategies (Putman 1996). Moose are

known for their long-distance migration patterns between winter and summer areas, this behavior has proven to increase reproductive performance by utilizing better summer areas (Rolandsen et al. 2017). Roe deer is less known for moving great distances between seasons but is however moving according to available food resources (Cagnacci et al. 2011,), however, roe deer could partially change movements pattern during winter as a response to changing forage availability. Red deer have been shown to be both migratory and stationary in response to seasonal changes (Boyce 1991; Martin et al. 2018), however, due to supplemental feeding this migratory behavior may stop (Jones et al. 2014). With this knowledge, habitat selection will ultimately be affected by seasonal variations in food requirements and availability. If movement patterns are affected by other ungulate species density, this may also alter species habitat selection where competing species coexist (Perez-Barberia et al. 2013).

Inter- and intra-specific recourse competition between ungulates has been shown to be affected by whether the species is a browser, mixed feeder or grazer (Spitzer 2019). Intra-specific competition was more common for moose who is a browser whilst red deer and roe deer, as a mixed feeder, had greater dietary plasticity and therefore no obvious intra- or inter-specific competition was clear (Spitzer 2019). However, dietary overlap was highest for all three species during winter and spring, when the diet consisted of mostly woody browse, except for moose and red deer which had the highest dietary overlap during autumn. These findings demonstrate that habitat selection depending on season of the year might be affected by resource overlap between sympatric species.

Besides having different feeding strategies regarding being a browser, mixed feeder or grazer, moose, red deer and roe deer also have differing herding behavior. Moose are mostly solitary throughout the majority of the year without being territorial, however, bulls sometimes gather in groups and females with calves or yearlings are common in sight (Jarnemo et al. 2018). Roe deer are more territorial, especially mature males, which usually occurs between early spring until late summer, during winter they are occurring in smaller groups for increased protection against predators (Jarnemo et al. 2018). Red deer are less solitary and are more commonly appearing in herds or groups, though often segregated between females and males (Jarnemo et al. 2018). Ungulates displaying dominant behavior can potentially be able to outcompete other less dominant species over the same food resource (Ferretti et al. 2012), this could then ultimately affect habitat selection for competing species. When species competition starts to affect food availability and quality, impacts on individual survivability and fitness may get influenced in negative ways such as decreased weight, fecundity and reproductive success (Corlatti et al. 2019). As preferred food resources decrease, they are forced to

choose second-choice forage (Spitzer 2019) as well as change roaming behavior if more time needs to be spent searching for food.
Time of day is an important factor influencing species activity and therefore also habitat selection. In a study by Coppes et al. (2017) they saw that red deer avoided human recreational trails during day but had a positive correlation during night. During warm hot summer days, moose is dependent on heat cover and spend more time foraging during the cooler nights (van Beest et al. 2012). As daylight hours differs substantially between seasons in northern Sweden, ranging from 3 hours up to 21 hours in the southern part of northern Sweden, habitat selection influenced by time of day becomes more difficult to predict further north one look.
The aim for this thesis is to understand how roe deer, red deer and moose interact and select habitat in relation to each other and respond to each other's density. Specifically, I investigate: (1) What determines habitat selection at landscape scale? (2) What determines seasonal habitat selection? (3) What determines diurnal habitat selection? (4) How do these species respond to each other's density in space and time – do they select or avoid areas of high density of sympatric species?

These are the hypothesis I derived for the questions above: habitat selection will differ between the three species due to known differences in foraging behavior, life history and diet (Spitzer 2019). I also suspect that seasonal habitat selection will be different due to changing availability in forage as well as increased overlap in habitat selection during winter and spring when food variability is low (Spitzer 2019). For red deer I expect selection for habitats during nighttime as the species is known for being more active during night (Godvik et al. 2009; Ensing et al. 2014). I also believe that density of other ungulates will affect species space use in the form of selection for lower density areas of each other due to differing herding and social behavior (Jarnemo et al. 2018). During winter when forage availability is lowest, I suspect that selection for low densities will not be as strong as for other seasons when resource availability if greater (Spitzer 2019).

In this study I will use integrated step-selection function (iSSF) (Avgar et al. 2016; Thurfjell et al. 2014) for modeling ungulate movements with telemetry data derived from GPS- collars on all three species and connecting these to habitat and density covariates created from pellet-count data and camera traps. With the results derived from these analyses, this knowledge could help wildlife managers in different work fields to create management plans with more aspects in consideration where these three ungulate species coexist. The focus will be to investigate how the density of these three ungulate species affect one another by quantifying movement ecology and reconnect to habitat selection, which plays an important role in intra- and interspecific competition (Putman 1996).

2. Material and method

2.1. Study area

. The study area, called as Järnäshalvön, is a peninsula located in the northern Swedish province of Västerbotten (Figure 1). The study area is ca 200 km2 and borders towards the Bothnian bay on three sides, the northern fourth side is cut off by a fenced highway and railroad. What makes this area unique in Europe is that it is inhabited by four different ungulate species, red deer, roe deer, fallow deer (*Dama dama)* and moose which coexist in a heterogeneous landscape consisting of boreal forest, agricultural land, mires as well as human settlements.

This area has been used in this study to estimate ungulate densities by using camera traps and pellet counts. In a study carried out by Pfeffer et al. (2018) that used the same area for camera trapping and pellet cunts, they concluded that minimal movement of ungulates between the study area and the mainland takes place which lead to exclusion of data outside of the study area. Supplemental feeding also takes place in this area during winter.

2.2. Data collecting

2.2.1. Pellet count and camera trapping

To estimate the spatial pattern of ungulate densities, pellet count data and camera traps was used. The pellet counts are done right after snow melt in spring, usually in May-June. This data was collected during the years 2015, 2016, 2017 and 2018 as they are a part of an annually pellet count survey. Pellet counts is based on removing present pellet groups of the study animal in a stationary sample plot (Figure 1) and later return (depending on what is being studied) to count the number of pellet groups that has appeared. Knowing the number of pellet-groups the study animal leaves each day, species densities over an area can be estimated. When using pellet counts to estimate species densities, pellet size and detectability of the pellets

influence density estimates (Pfeffer et al. 2018). The data was collected on an established sampling grid where each sampling plot had a radius of 5,56 m (plot size= 100 m2,)

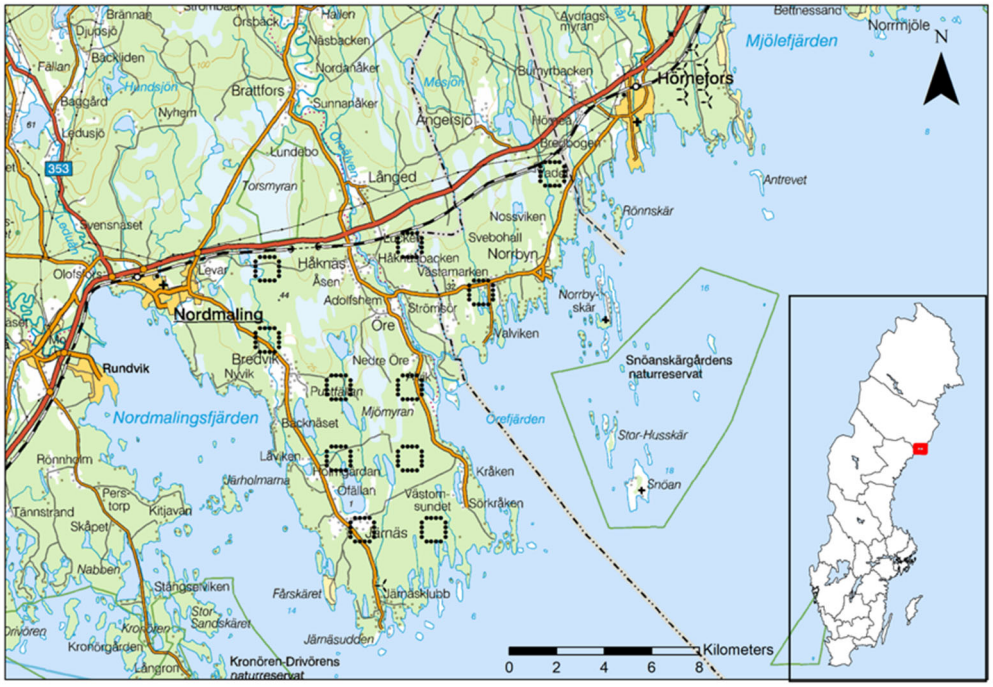

Figure 1. Grid map over the positioning of the stationary pellet count sample plots in Järnäshalvön Each black dot represent the sample plots in this study

Pellet groups from each species, red deer, moose and roe deer were collected and identified according to their morphological characteristics and later validated using DNA methods (Spitzer et al. 2019). Since roe deer and fallow deer (which also occur in the same area) pellets was difficult to distinguish, the number of pellets per dung group was used to distinguish the two species. Pellet groups containing >45 pellets were considered fallow deer and groups with □45 pellets were considered as roe deer. The ability to identify which species each pellet group belongs becomes more difficult the more diverse the ungulate community becomes. Bias in density estimates of smaller species could be more common due difficulties in detecting pellets as well as species identification (Pfeffer et al. 2017).

The design of the camera distribution consisted of 11 squared transects, each 4 km, evenly distributed over the study area (Figure 2). At each transect, 18 locations for camera traps were chosen with 100 m apart. Between 29 January 2017 to 14 February 2014, a total of 198 locations were sampled but due to camera

malfunction, fallen tree and wrong placement of camera, 193 locations were used in the analysis.

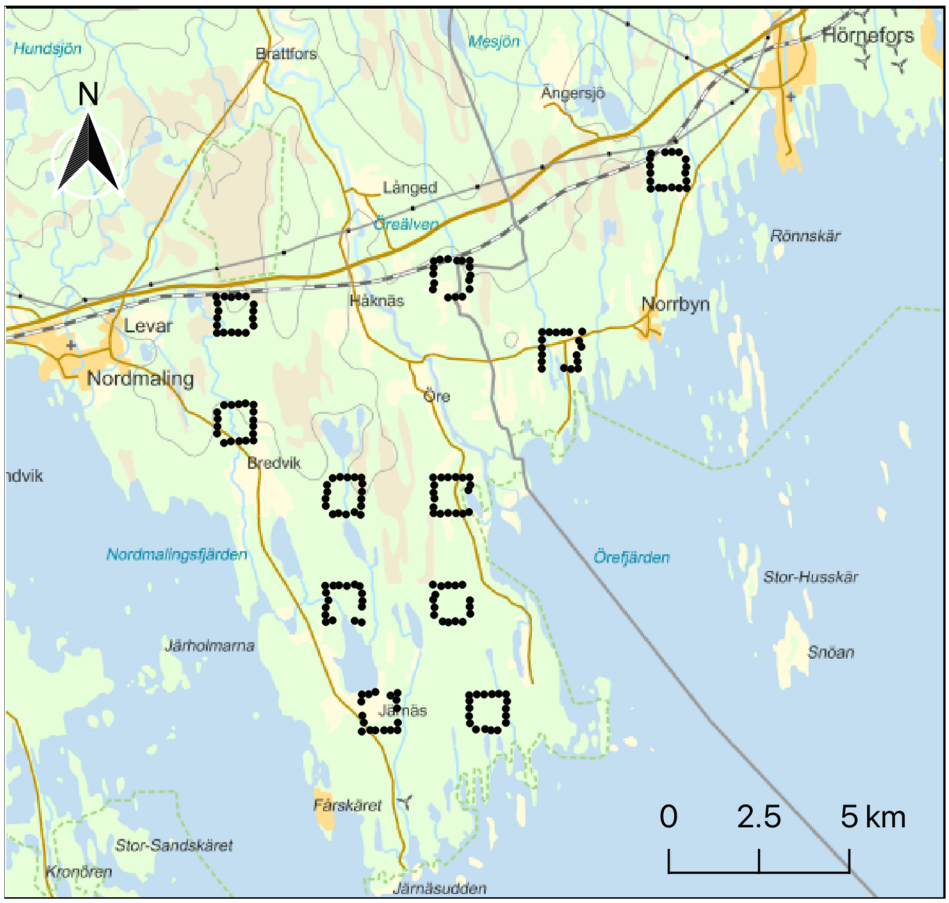

Figure 2. Grid map of positioning of camera traps in Järnäshalvön. The black dots represent each of the 193 cameras sampled in the study.

Plots that were sampled <100 m from human settlements or roads were excluded due to permit restrictions. In addition, sampled plots in lakes and fields where the camera could not be properly mounted on existing trees were also excluded. At each plot, a suitable place was chosen where at least 10 m of clear view could be attained in front of the camera to avoid natural features to affect the detectability. The cameras were further mounted 1 m above the ground in order to avoid heavy snow and in addition, distances of 5 m, 10 m and 15 m were marked in front of the camera's central view with red ribbons. The cameras used in this study took three rapid-fire pictures when triggered which allows for a recording of the full passage of an animal through the detection zone. Moreover, each camera was set to take a control picture every day to ensure full functionality throughout the study period. One downside with using camera traps is the detectability regarding species identification as well as sex/individual of an animal. By-catch data is also inevitable

with this type of method, potential use to quantify climatic parameters and timing of plant phenology with this data has been highlighted in a study by Hofmeester et al. (2019). Home-range size of the species also affects the detectability where increased home-range size lowering the detectability. Due to these downsides, criticism has been directed towards the use of camera traps for estimating species densities.

2.2.2. Telemetry data

In this study, telemetry data was derived from GPS collars on three of the three ungulate species involved in this study. Data could only be collected from moose, roe deer and red deer and additionally, all individuals equipped with collars were females. Roe deer collars only lasted for a year but for moose and red deer the collars could stay on longer before they fell off automatically. In this study, data was derived from year 2017-2019 for roe deer, year 2018-2019 for red deer and 2017-2018 for moose. Seven red deer, 27 moose and 23 roe deer were included in this study. Positioning recording ranges from 20 min intervals up to 6 h with an average of 30 min for roe deer and 1 h for moose and red deer. The GPS collars was of the type Vectronic-Aerospace and differed in size between the species, moose had 7D battery, red deer 3D battery and roe deer 1D battery. All data recorded from the collars goes to a database called WRAM at SLU (Swedish University of Agricultural Sciences).

2.3. Analysis

2.3.1. Integrated step-selection function

Integrated step-selection function (iSSF) can be used to link animal movement consisting of telemetry data to environmental covariates such as habitat features to answer questions regarding movement behavior (Avgar et al. 2016; Thurfjell et al. 2014). In this study I used both a land use raster derived from the Swedish land surveying agency (www.lantmäteriet.se) as well as density raster for each ungulate species in the study area to link with the telemetry data. Furthermore, iSSFs was estimated by comparing observed steps, in the form of consecutive GPS-locations, to random steps using likelihood equivalent of a Cox proportional hazards model which in turn is linked to a habitat- or ungulate density covariates (Avgar et al. 2016). To be able to link habitat and density covariates to the telemetry data, step length and turn angle for each step was generated to generate random steps to compare with the observed steps/locations (Thurfjell et al. 2014).

For the step-selection analysis a package in R-studio (R core team 2019) called 'amt' (animal movement tools) was used to fit iSSF to the telemetry data and derive regression coefficients as a result of habitat use and density responses of animals from fitted models (Signer et al. 2018). The amt-package contained the tools to extract random steps from each known GPS-location and furthermore compare these random steps associated with the covariates with observed steps associated with the same covariates (Signer et al. 2018). Random steps were generated with a tool within the amt-package which fits gamma distributions to the step lengths and Von Mises distributions to the turn angles using maximum likelihood (Signer et al. 2018). In this study 10 random steps were generated for each observed step. Covariates was then extracted for each step (random and observed) to finally fit the conditional logistic regression model with the tool fit_ssf within the amt-package which in turn generated regression coefficients (Signer et al. 2018). In addition, the tool time_of_day was used to generate diurnal information for each step in the form of day or night to test if habitats are selected for during day or night.

2.3.2. Land-use patterns

Land use class covariate was used to test hypothesis regarding spatio-temporal habitat use in relation to season of the year. Season of the year influences habitat use for many ungulate species, especially in boreal landscapes where the climate and recourse availability differ substantially between seasons (Spitzer 2019).
In order to evaluate seasonal movement patterns in response to habitat availability in this study, a raster with land cover data was used as a covariate for each species and season. This raster was divided into six categories consisting of "forest", "agricultural land", "clear cut" (deforested areas with forest height of less than 5 m), "open land" (non-forest open land other than clear cuts), "wetland", "water" (lakes and sea) and "other" (human settlements and urban areas) (Table 1). The four different seasons was divided as winter (November-March), spring (April-May), summer (June-August) and autumn (September-October). These categories were chosen so as to reflect the classes that are relevant to deer species.

Grid code	**Class**	**Reclassified to:**
111	Pine forest not on wetland	Forest
112	Spruce forest not on wetland	Forest
113	Mixed coniferous forest not on wetland	Forest
114	Mixed forest not on wetland	Forest
115	Deciduous forest not on wetland	Forest
116	Deciduous hardwood forest not on wetland	Forest

117	Deciduous forest with deciduous hardwood forest not on wetland	Forest
118	Temporarily non-forest not on wetland	Clear cut
121	Pine forest on wetland	Forest
122	Spruce forest on wetland	Forest
123	Mixed coniferous on wetland	Forest
124	Mixed forest on wetland	Forest
125	Deciduous forest on wetland	Forest
126	Deciduous hardwood forest on wetland	Forest
127	Deciduous forest with deciduous hardwood forest on wetland	Forest
128	Temporarily non-forest on wetland	Clear cut
2	Open wetland	Wetland
3	Arable land	Agricultural land
41	Non-vegetated other open land	Other
42	Vegetated other open land	Open land
51	Artificial surfaces, building	Other
52	Artificial surfaces, not building or road/railway	Other
53	Artificial surfaces, road/railway	Other
61	Inland water	Water
62	Marine water	Water
0	Outside mapping area	Other

Table 1. Grid codes and classification of the national land cover raster with associated reclassification.

2.3.3. Density covariates

By using pellet count data and camera trap data, ungulate density rasters were derived by interpolating the spatial points generated from these data which then further were interpolated onto a forest-cover raster with the resolution 1x1 km. A raster with density information in the form of high-medium-low was created for each species using package gstat in R-studio which then later could be used to fit the telemetry data by fitting iSSF to the density covariates.

Package gstat was used to interpolate pellet-count and camera trap data onto the forest cover raster with resolution 1x1 km giving density information in numeric format in each grid for each species (Figure 3). The classification of the density raster was chosen with regard to relevance and inclusion of variables for later discussion of the results.

Movement patterns in relation to other ungulate densities was tested, and each model was divided into four seasons; winter, spring, summer and autumn. Separating the models in response to season was done in regard to differing habitat use and recourse requirement (Spitzer 2019). Northern Sweden is characterized by big changes in temperature and recourse availability between seasons, leading to the inclusion of this variable in this study as a potentially important factor.

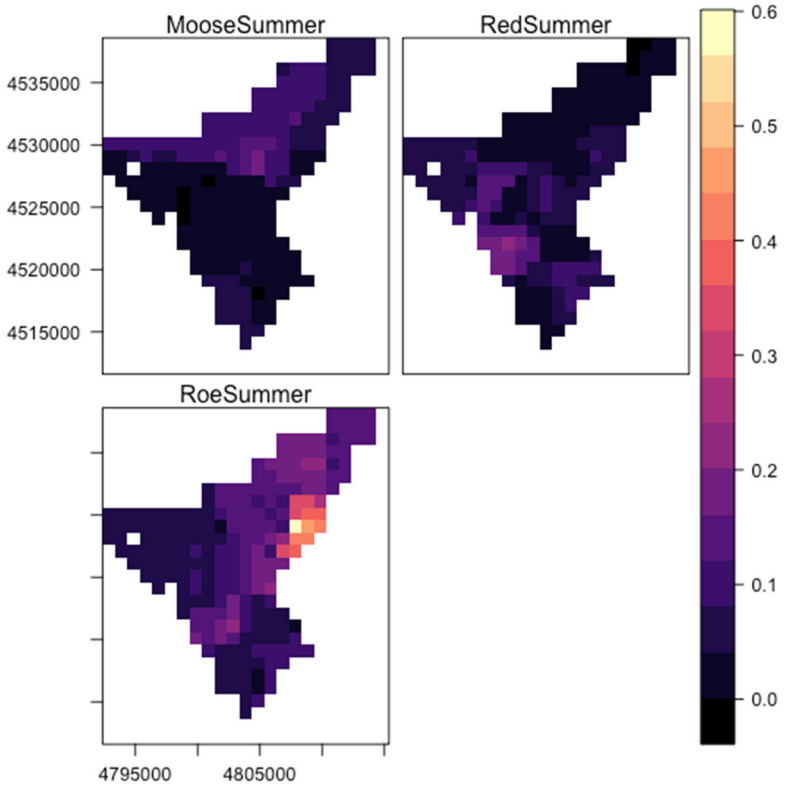

Figure 3. Density heatmaps generated with package gstat in R-studio for moose, red deer and roe deer during season summer in unit number of animals/km^2. Used as density covariates when fitting iSSF to make conclusions about how ungulate movement is affected by other ungulates densities.

3. Results

3.1. Ungulate habitat selection over the full year

Species	Observations	Observations/individual
Moose	333212	12341
Roe deer	77662	3377
Red deer	18882	2697

Table 2. Number of sampled observations per species and individual.

Moose
Over the whole year, moose selected for clear-cut areas (coefficient 0.5, z-value 5.33, $p<0.01$) and open land (z-value 26.59, $p<0.01$) (Figure 4) (Appendix 3).

Red deer
Red deer selected for clear-cuts (coefficient 0.81, z-value 16.51, $p<0.01$), wetlands (coefficient 0.26, z-value 2.82, p-value $p<0.01$), agricultural land (coefficient 0.59, z-value 4.3, p-value 1.75e-05) and open land (coefficient 0.34, z-value 3.6, p-value $p<0.01$) (Figure 4) (Appendix 2).

Roe deer
Roe deer selected for clear-cuts (coefficient 0.12, z-value 3.37, p-value $p<0.01$), agricultural land (coefficient 0.21, z-value 3.76, p-value $p<0.01$) and open land (coefficient 0.24, z-value 4.71, p-value $p<0.01$) (Figure 4) (Appendix 1).

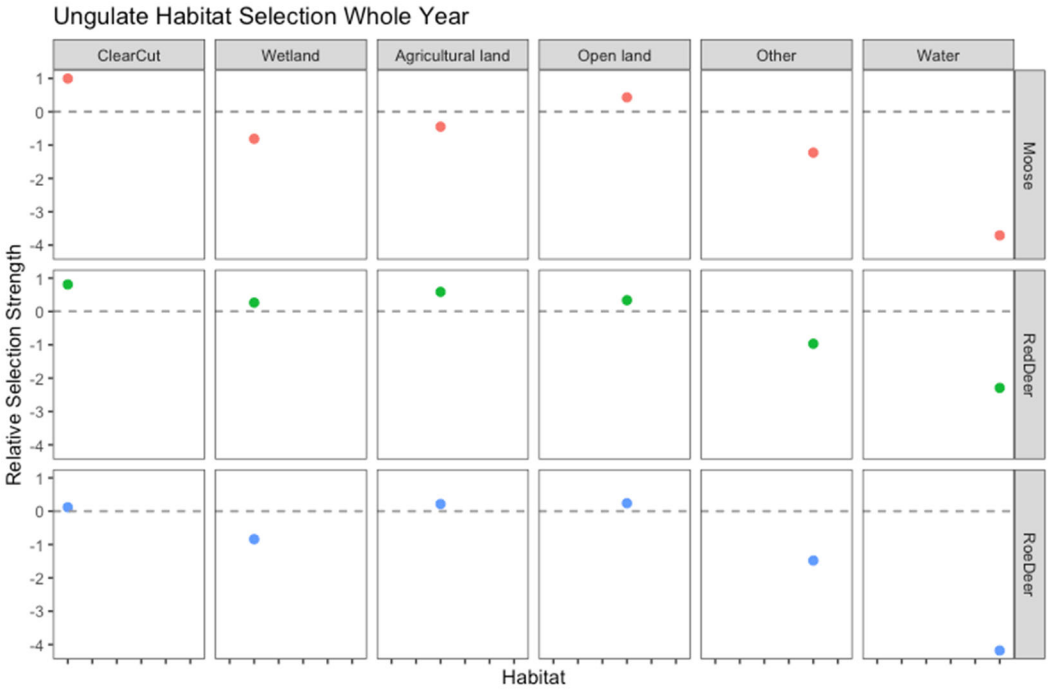

Figure 4. Habitat selection for roe deer, red deer and moose during the whole year with forest habitat as response variable (0).

3.2. Habitat selection depending on season of the year

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Species	Spring	Summer	Autumn	Winter
Moose	38630	14022	45955	434605
Roe deer	5509	3726	82	9565
Red deer	8836	9670	2864	56292

Table 3. Number of sampled observations for each species and season.

Spring

In Spring, moose selected clear-cuts over forests (0.51, z-value 12.77, $p<0.01$) (Figure 5) (Appendix 6). For red deer (Appendix 5) and roe deer (Appendix 4), agricultural land was more likely to be selected over forests (Red-1.05, z-value 10.09, $p<0.01$; Roe - 0.19, z-value 1.89, $p<0.01$, (Figure 5).

Summer

Moose selected for clear-cuts (0.66, z-value 10.84, $p<0.01$) (Figure 5) (Appendix 6) during summer. Red deer and roe deer had a more diverse selection than moose

(Figure 5) (Appendix 4;5). Red deer selected for clear-cuts (0.88, z-value 12.56, p<0.01), wetland (0.92, z-value 8.95, p<0.01) and open land (0.73, z-value 6.71, p<0.01). Roe deer selected clear-cuts (0.64, z-value 9.30, p<0.01), agricultural land (0.61, z-value 4.74, p<0.01) and open land (1.00, z-value 10.88, p<0.01) during summer (Figure 5).

Autumn

During autumn moose selected clear cuts over forest (Figure 5) (Appendix 6). Red deer selection during autumn was inconclusive due to large confidence limit (appendix 5). Roe deer selected agricultural land (coefficient 0.52, z-value 3.01, p<0.01) slightly more over forests (Figure 5) (Appendix 4).

Winter

Moose and selected clear-cuts during winter (coefficient 0.54, z-value 9.35, p<0.01, Figure 5) (Appendix 6). Red deer results were inconclusive due to large confidence limit (Appendix 5). Roe deer did not select for any other habitats over forested land during winter (Figure 5) (Appendix 4).

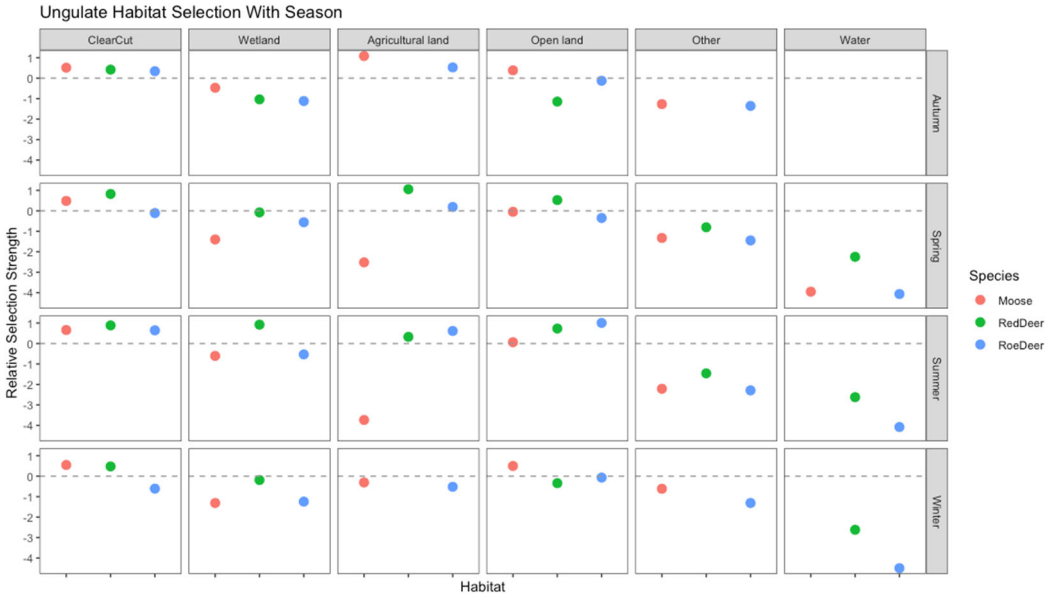

Figure 5. Habitat selection depending on season of the year for roe deer, red deer and moose with habitat forest as response variable (0).

3.3. Diurnal habitat selection over the full year

Moose

Moose movement pattern was mostly directed towards day for the majority of the habitat types (Figure 6) (Appendix 9).

Red deer

Red deer movement pattern was directed towards night for the majority of the habitat types (Figure 6) (Appendix 8), in contrast to moose.

Roe deer

Roe deer movement pattern was directed towards day for the majority of the habitat types (Figure 6) (Appendix 7).

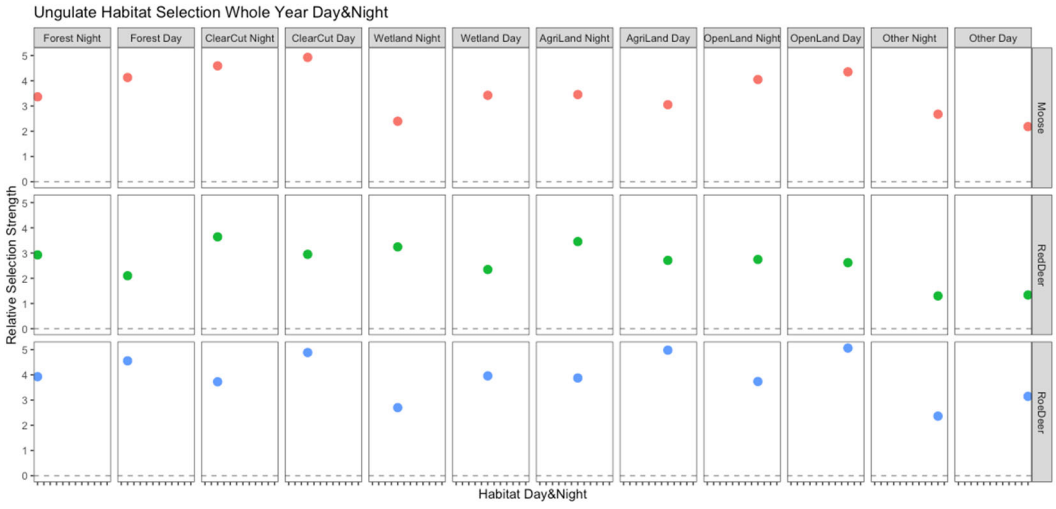

Figure 6. Habitat selection for roe deer, red deer and moose during the whole year depending on time of day.

3.4. Ungulate habitat selection depending on season of the year and time of day

Moose

For moose, forest, wetland, clear-cut, open land and other was more selected for during the day in spring (Figure 7) (Appendix 12). Agricultural land was in contrary to the other habitats more selected for during the night in spring.

Red deer

For red deer, wetland was the only habitat type more selected for during the day whilst the other habitat types were more selected for during the night in spring (Figure 7). During summer, red deer selected forest, clear-cut, wetlands, open land

and other more at daytime, however, agricultural land was more selected for during the night. Nighttime were more selected regarding all habitat types during winter for red deer (Figure 7) (Appendix 11).

Roe deer

During spring, roe deer selected for forest, clear-cut, wetland, agricultural land and open land during daytime (Figure 7). Habitat type "other" was more selected for during the night in contrast to the other habitat types during season spring. In summer, roe deer selected all habitat types during daytime with lowest selection strength towards habitat type "other" (Figure 7). Selection depending on time of day was the most variable during winter where roe deer selected for forest slightly more during nighttime, clear-cut during daytime, wetland during daytime, agricultural land during daytime, open land during daytime and habitat type "other" during night (Figure 7) (Appendix 10).

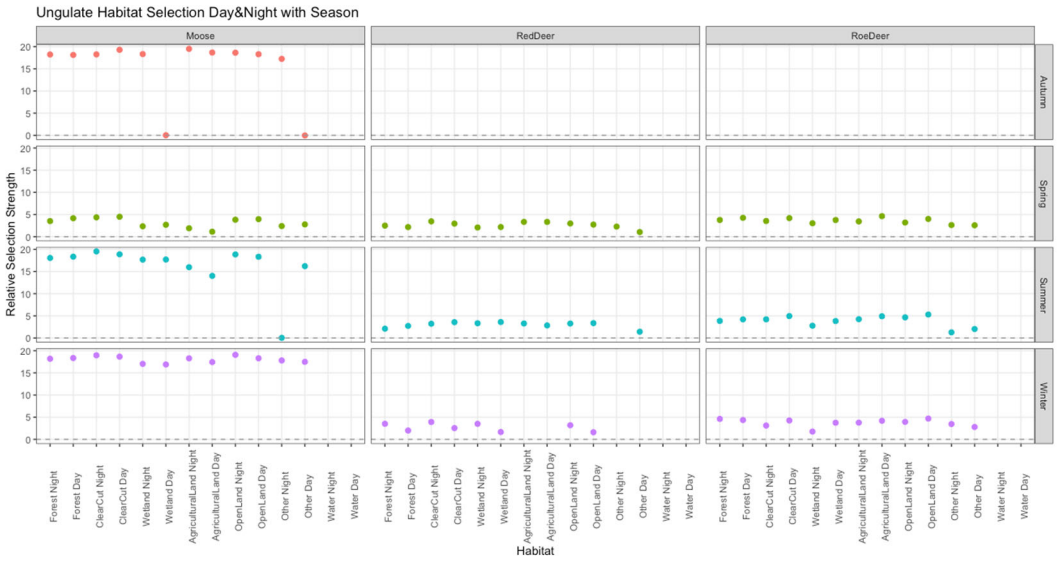

Figure 7. Habitat selection for roe deer, red deer and moose during day vs night and season of the year.

3.5. Ungulate movement response species density over the full year

All results derived were against high density. High density was used as response variable to be able to make conclusion on if the different species select for lower densities of other ungulates or not. Some results regarding density responses for roe deer and red deer was not possible to derive in the iSSF analysis.

Roe deer

Roe deer consistently selected for areas with low and/or medium moose density (coefficient 2.76, p<0.01, z-value 6.71 and medium coefficient 2.73, p<0.01, z-value 6.64, Appendix 13) over the full year.

Red deer

Red deer had not directed selection for low densities of roe deer over the full year (Appendix 14).

Moose

Moose had no directed selection to areas with low or medium red deer densities and selected for areas with low (coefficient 1.20, p-value p<0.01, z-value 3.84) and/or medium roe deer densities (coefficient 1.23, p-value 0.0117, z-value 3.92, Figure 8).

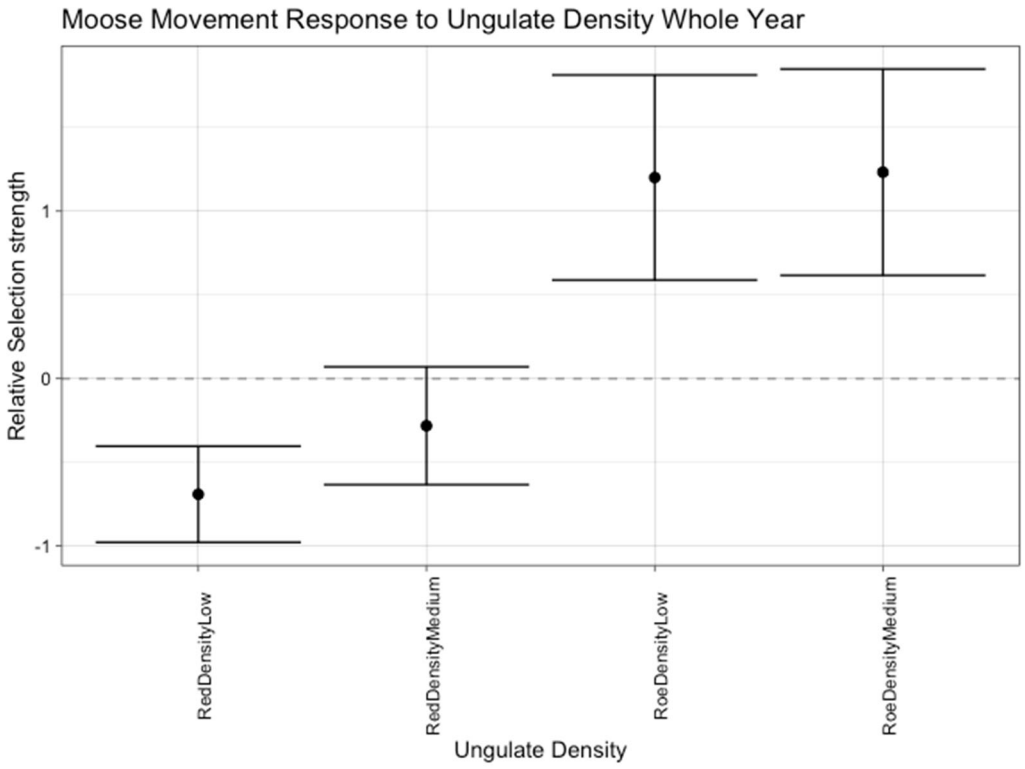

Figure 8. Moose movement response to red deer and roe deer density during the whole year with high density as a response variable.

3.6. Ungulate movement response to species density depending on season of the year

By adding season as a variable in the analysis, there were too few data points matching with the density covariates in the iSSF analysis for some of the seasons and species regarding all three species. All results derived were against high density.

Spring (Roe deer)
In spring, roe deer selected for medium densities (coefficient 0.38, p-value 1.40e-03, z-value 3.19) of moose and low densities (coefficient 0.66, p-value $p<0.01$, z-value 3.44) of red deer were also selected for during the same season (Figure 9). Due to confidence interval spreading over both negative and positive selection for low densities of moose, the result was inconclusive.

Summer (Roe deer)
Roe deer avoided low and medium densities of moose during summer (Figure 8).

Autumn (Roe deer)
During autumn, roe deer response to moose were inconclusive due to confidence interval spreading over both positive and negative selection (Figure 9).

Winter (Roe deer)
During winter, roe deer selected for low (coefficient 3.18, z-value 7.10, $p<0.01$) and medium densities of moose (coefficient 3.64, z-value 8.10, $p<0.01$) (Figure 10). Roe deer also selected for low densities of red deer (coefficient 3.13, z-value 6.97, $p<0.01$) and medium densities was selected for (coefficient 3.83, z-value 8.55, $p<0.01$) (Figure 9).

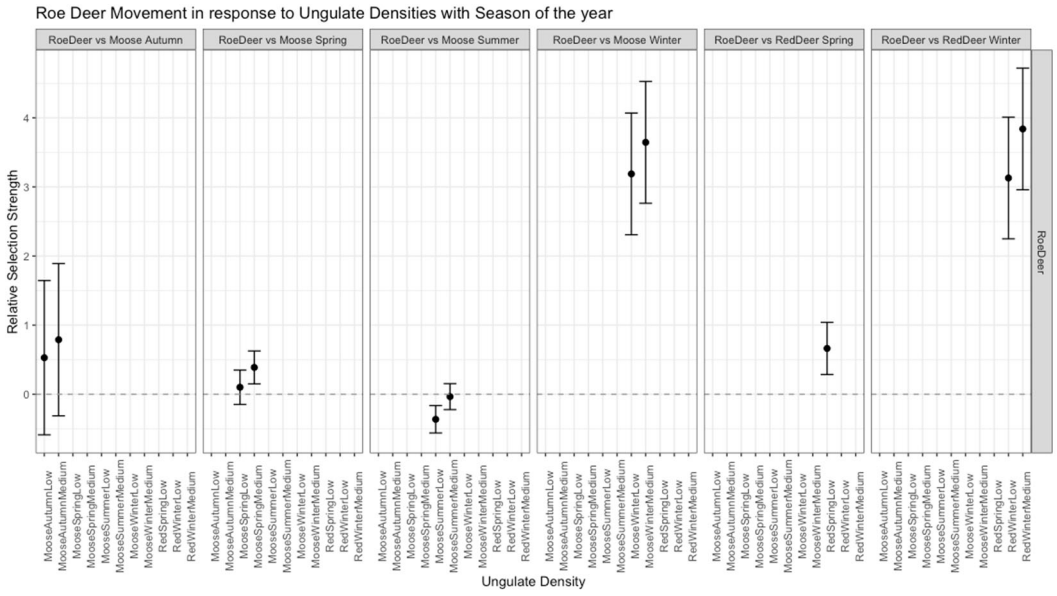

Figure 9. Roe deer movement in response to red deer and moose densities depending on season of the year with high density as response variable.

Autumn (Red deer)

During Autumn, red deer had no directed selection towards medium densities of red deer and responses to low densities got inconclusive due to large confidence interval (Figure 10).

Winter (Red deer)

During winter, red deer selected for medium densities of moose (coefficient 0.41, z-value 4.06, $p<0.01$) and had no directed selection towards low densities. Low densities of roe deer were selected for (coefficient 0.49, z-value 3.44, $p<0.01$) by red deer and medium densities were also selected for, however, the confidence interval makes it inconclusive (Figure 10).

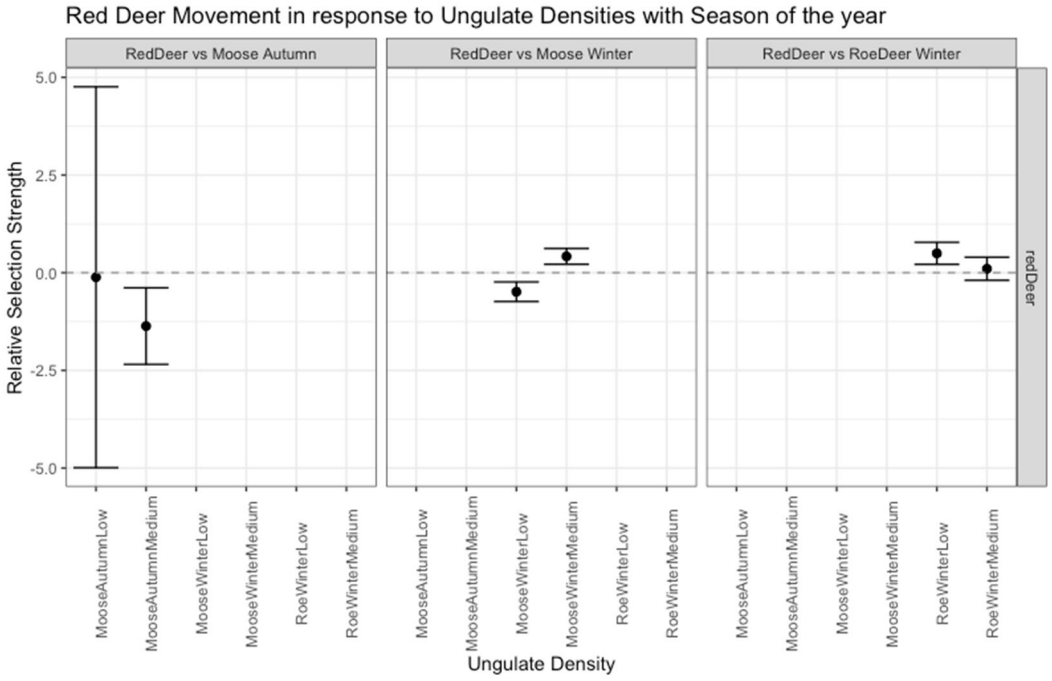

Figure 10. Red deer movement in response to roe deer and moose densities depending on the season of the year with high density as a response variable.

Summer (Moose)

During summer the results derived was inconclusive due to large confidence interval (Figure 11).

Winter (Moose)

During winter, moose had no directed selection towards low and medium densities of red deer. Low and medium densities of roe deer results was inconclusive due to large confidence interval (Figure 11).

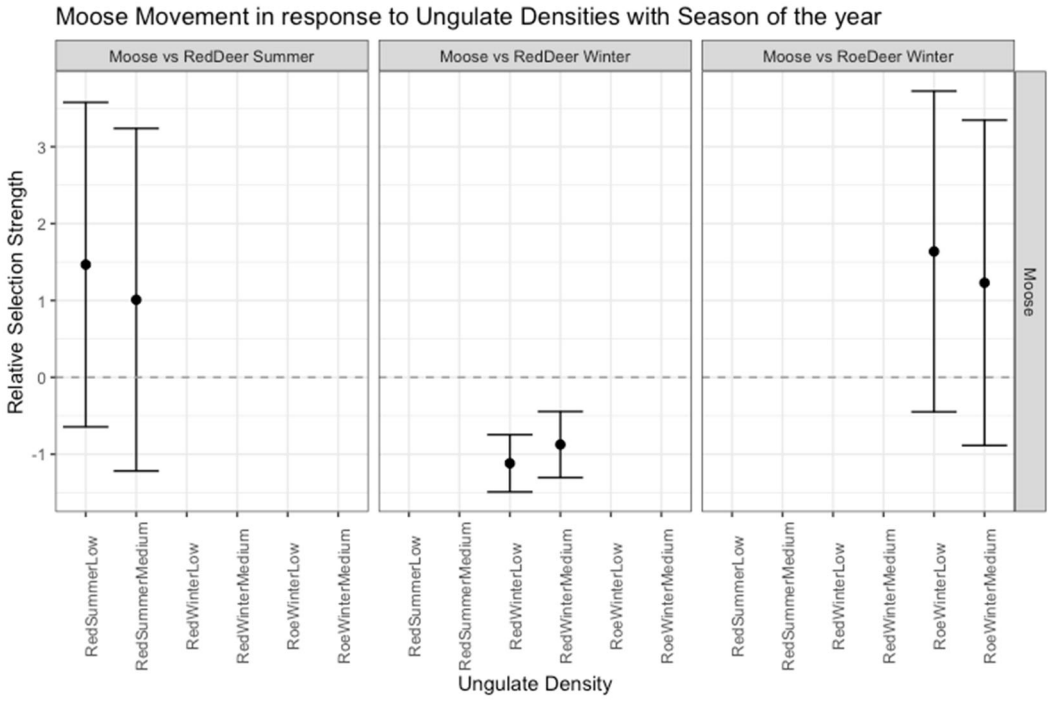

Figure 11. Moose movement in response to roe deer and red deer densities depending on season of the year with high density as response variable

4. Discussion

In this study the result showed that moose, roe deer and red deer movement pattern selected clear-cut areas rather than forested areas during both summer and autumn Red deer had the most variable habitat selection over forested areas, compared to the other two species, and was also selecting for the majority of the habitats during night. In contrast to red deer, both moose and roe deer selected the majority of the habitats during day. However, during summer, red deer also selected the majority of the habitats during day. These results imply that habitat overlap occurs and potential competition for resources. Densities of other ungulates clearly affected species movement patterns in the form of selection of low/medium densities of other ungulates. Moose and roe deer both selected for low/medium densities of each other whilst red deer had no directed selection towards low densities of roe deer.

4.1. Habitat selection

Over the full year moose movement pattern indicated selection for clear-cut and open areas over forested land, this could be as a response to preferred forage in these types of habitat (Figure 2) (Jarnemo et al. 2018). These areas also contain more edges which often provides a mixture of different types of food choices such as young shoots, herbs and seedlings from deciduous trees. Since all tagged animals in this study was females, a possible explanation for moose to choose relatively open areas could be to that females often are followed by a calf and therefore needs areas with good overview of their surroundings as well as high quality food (Bjorneraas et al. 2012).

Red deer had the most variable habitat selection in relation to forested land, as for moose, clear-cut had the strongest selection over forested land, and agricultural land as the second most selected habitat (Figure 2). This, as for moose again, could be a response preference to high quality food in areas like these. The fact that red deer had more variable habitat selection than moose is not surprising since red deer is known to have a more variable diet as mixed feeders (Putman 1996, Spitzer 2019). However, the fact that red deer seems to prefer agricultural land over forested land

could be of potential interest for crop-owners if potential damage is appearing in areas where red deer is present. For roe deer, as for both moose and red deer, clear-cut and open land was more selected for than forested land. In contrast to moose, roe deer selected for agricultural land, the same as for red deer (Figure 2).

The results from the habitat selection over the full year indicates potential overlap in clear-cut areas as well as for open land (vegetated and unvegetated) (Table 1) regarding all three species. Red deer and roe deer movement pattern in selection of habitats overlapped more often than with moose respectively. Moose had the strongest selection for clear-cut over forested land than the other two species. This confirms previous studies on how young forest stands are preferred as source of food for moose (Wam et al. 2010). Red deer as a mixed feeder might be more adaptable when preferred food resources are absent and are able to switch to feed more like a browser (Spitzer 2019). This however could lead to increased overlap with roe deer and moose who is browsers to begin with, browsers seem to not have the dietary plasticity as mixed feeders have (Spitzer 2019). My hypothesis regarding differing habitat selection in response do differing diet was somewhat confirmed, however, there was overlap in habitat selection regarding moose and red deer even though they have differing feeding strategies. As mentioned above, this could be as a consequence of red deer's diet plasticity as well as less food choices in northern Sweden. Red deer and moose are both bigger in size than roe deer, giving them the advantage of coping with higher snow depth in search of food. Roe deer, with its small size compared to red deer and moose, are less mobile in deep snow. Therefore, during winter when snow depth can be deep, roe deer is restricted to areas with less snow, for example forest. This could explain why roe deer seem to avoid other habitat types during winter.

My hypothesis regarding differing habitat selection in response to season of the year was confirmed, seasonal changes in habitat selection was showing for all three species. Moose showed selection for agricultural land and open land during autumn, one potential reason for this could be that rutting season happens during late September and yearly October (Jarnemo et al. 2018). However, selection results regarding habitat wetland, other and open land had large confidence limits spreading over both selection and no directed selection (Appendix 6), rutting behavior might influence these insecurities in the result. During rutting season, habitat selection with best forage is no longer a priority, instead finding a mate is. Rut occurs during autumn for red deer (Jarnemo et al. 2018), so similar large confidence limits spreading over selection and no directed selection of clear-cut, wetland and open land. One might therefore not be able to make any conclusions on whether their habitat selection is due to forage but instead what habitat is preferred during rut. Due to few data points for red deer during autumn, agricultural

land, other and water could no longer be reliable. However, clear-cut was still preferred over forested land. Roe deer showed strongest selection for agricultural land over forested land during this time of the year, one explanation might be that agricultural land during this time of the year is now the greenest areas and some farmers maintain hay fields, especially when all the leaves has fallen of the trees, generating the best/easiest source of food.

The movement pattern for moose during spring displayed selection for clear-cut over forested land. Red deer showed a variable selection, selecting for clear-cut, agricultural land and open land over forested land during the same season. Roe deer had the least variable selection over forested land with a weak selection of agricultural land. This result could be a consequence of high snow depth when data was collected, leading to roe deer spending more time under forest canopy where snow depth is lower, making it easier for the deer to forage. This could be a possible reason due to the same result during winter where roe deer also showed a weak selection for agricultural land over forested land. These results do not coincide with my hypothesis that potential overlap in habitat selection during spring could be visible due to few available food choices. Spitzer 2019 found that roe deer increased their brows on Vaccinium spp. when the density of other ungulates was high, this could be a potential reason why roe deer seems to avoid other habitats over forested areas as forested land with coniferous trees inhibits Vaccinium spp.

During summer, moose and red deer showed similar selection of habitats as during spring. However, roe deer showed a much more variable selection over forested areas during summer than during spring, perhaps compensating for its inability to move around in variable habitats during winter and spring. Once again, moose overlap in movement and selection for clear-cut areas with the other two species.

Winter habitat selection was fairly similar for red deer and moose where clear-cut was selected for, however, red deer was lacking results for selection of agricultural land and habitat type other. The lack of results could be due to too few data point matching in the analysis. Red deer also displayed movement towards open land during winter. One reason for this could be that supplemental feeding often takes place on open land and therefore is selected for during winter. Open areas are usually covered in snow during winter in northern Sweden. Roe deer showed no directed selection of the majority of the habitat types, except for a weak selection for open land. This could be due to the thermal cover forest gives and snow cover is lower under forest canopy as well as milder local climate. For a small ungulate as roe deer, this habitat is favoring during winter when snow cover can be high in open areas whilst lower under forest canopy.

As for red deer, supplemental feeding taking place on open land might be the reason for this selection. These results contradict my hypothesis that dietary overlap during winter might be reflected in similar habitat selection. Since supplemental feeding is used in the study area, this might disturb the species natural habitat selection.

Moose and roe deer movement pattern was showing more activity during daytime, in contrast, red deer were more active in the majority of the different habitats during night. This confirms my hypothesis regarding red deer selecting for habitats during night. Since roe deer and red deer had the most similar variability regarding habitat selection, these two might also have the most advantage in avoiding each other's presence by utilizing these habitats during different times of the day. This potential advantage, of utilizing different habitats during different daytime hours, is only true if it is beneficial to avoiding each other's presence. This can be validated using activity pattern data in further studies.

Including season of the year to this analysis unfortunately led to missing results for season autumn regarding red deer and roe deer. For the results possible to derive, moose and roe deer showed the same selection for day over the majority of the habitat types during spring as well as red deer selecting for nighttime. However, during summer, both red deer and roe deer selected for the majority of the habitat types during day, possibly due to short periods of darkness during summer in the northern Sweden. During winter, red deer showed movement patterns towards selecting for all habitat types during night. In contrast, roe deer selected the majority of the habitat types during day, except for habitat type "other", which includes human settlements, was selected for in night. A reason for roe deer, as well as moose and red deer, to select human settlements and urban areas during night might be as a response to humans being less active during night. Roe deer also selected for forest during night. My hypothesis regarding season of the year affecting movement patterns was true.

4.2. Ungulate movement response to species density

For the full year, roe deer selected for low and medium densities of moose. This could be due to exploitation of different types of forage between the two species displayed in the results regarding habitat selection, and/or due to direct avoidance (Spitzer 2019). Unfortunately, the data used for the analysis with density covariates was not enough to give results for how roe deer responds to red deer densities.

The limitations of the data were even greater for the analysis regarding red deer response to moose and roe deer densities over the full year since red deer had fewest

data points possible to work with (Table 2). Red deer displaying no directed selection of low densities of roe deer were the only result possible to derive for red deer response to ungulate densities. This means that low densities of roe deer did not affect red deer movement pattern.

Moose actively moved towards low and medium densities of roe deer. No directed movement patters towards low/medium densities of red deer were showing. As discussed above, these responses to roe deer and red deer might be due to contrasting habitat selection over the full year as well as differing diet choice (Spitzer 2019).

My hypothesis regarding species movement responses to other ungulate densities was true, selection for low/medium densities were derived for all three species. These results could indicate that differing social and/or territorial behavior lead to these species avoiding interactions with each other. Another possible explanation could be that overlap in forage since all three species had the strongest selection for clear-cut areas during the majority of the seasons (Figure 5). During winter, red deer had the strongest selection for medium densities of moose which confirms my hypothesis. Red deer selected for low densities of roe deer during winter, which could be due to red deer and roe deer selecting for differing habitats during winter (Figure 5). The movement pattern of moose was not affected by low/medium densities of red deer, this result validates my hypothesis that similarities in forage behavior during winter leads to these two species not being able to avoid each other. Roe deer selected for low/medium densities of both red deer and moose, in this case my hypothesis was not confirmed, however, looking at potential overlap in habitat selection during winter, roe deer stood out and was not overlapping with the other two species (Figure 5).

For further studies, higher resolution regarding density information on ungulate species could improve the ability to conduct analysis to answer questions regarding that type of information. With a resolution of 1x1 km used in this study, matching the telemetry data with much higher resolution – conclusions and significant results was difficult to generate when several variables were combined. However, since this is a rising topic, efforts in to investigate new ways of generating high resolution density rasters for this type of analysis should be of interest. In this study, pellet count and camera trap data were used to generate these density rasters, one way to increase the resolution could be to refine these data collecting methods to better match the telemetry data point resolution. The results from this study shows the potential versatile way of using iSSF to analyze movement patters of different ungulate species by combining different data collecting methods and use these results in modern ungulate multi-species management systems.

4.3. Conclusion

As mentioned in the introduction, multi-species management is becoming ever more common, especially where conflicting interests are involved. In order to prevent for example forest damage but still be able to keep a stable and plentiful population of game species, results from studies like this one could be of use. Since habitat selection is just one parameter affecting movement patterns- how different ungulate species interact in different environments is also key in multi-species management. This study also highlights the usage in combining different data collecting methods to broaden the ability to analyze ungulate movement patterns.

All species involved in this study are considered game species and are legally hunted in Sweden, this gives the opportunity to use hunting as a regulation of potential problems for forest or crop owners. However, hunters and landowners who wants to produce as much biomass as possible, usually have conflicting goals regarding densities of ungulates. Hunters usually want a stable population to harvest from while landowners wish to produce as much biomass as possible, want to have a small population. To be able to match these conflicting interests, results from studies like this one where habitat use, and species interactions are combined could be of potential use when it comes to which ungulate species to focus more or less effort on regulating depending on the goal in a certain area. Clear-cut areas appear to be an important habitat for the species involved in this study, second most favored habitat was agricultural land and open land. With this knowledge, complementing information on diet for each species and dietary responses with different deer densities will help to create management actions. Another important factor affecting habitat selection is recourse availability, if an area is more or less heterogeneous in forage, that areas ability to house several species with different dietary preferences becomes more or less possible (Macandza et al. 2012).

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Appendix 1

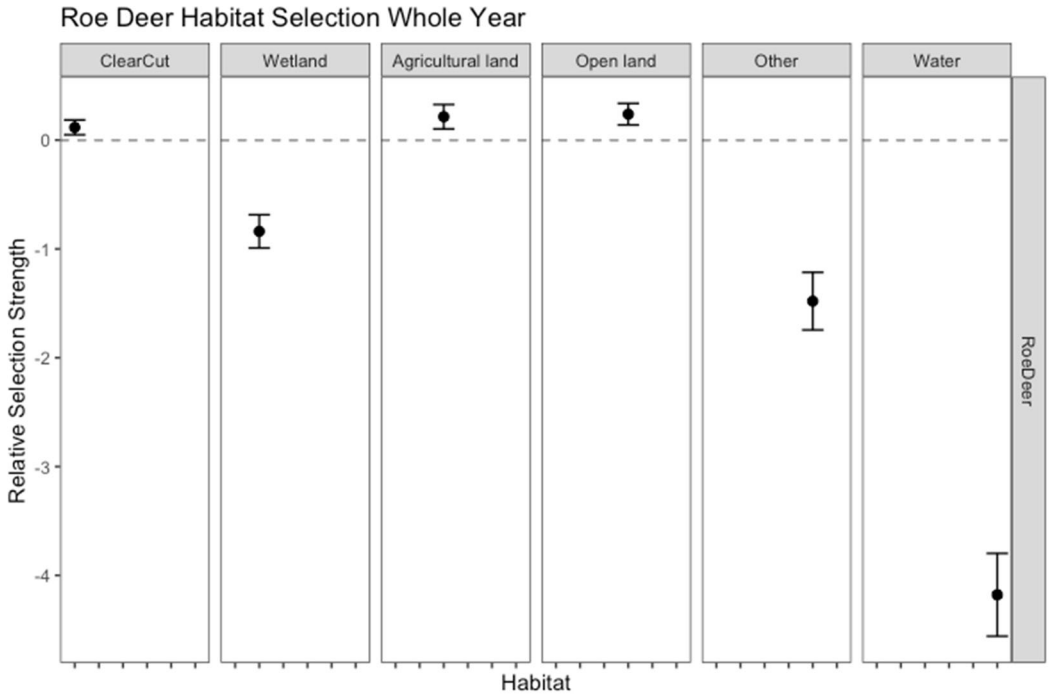

Figure 12. Roe deer habitat selection during the full year with habitat forest as response variable (0).

Appendix 2

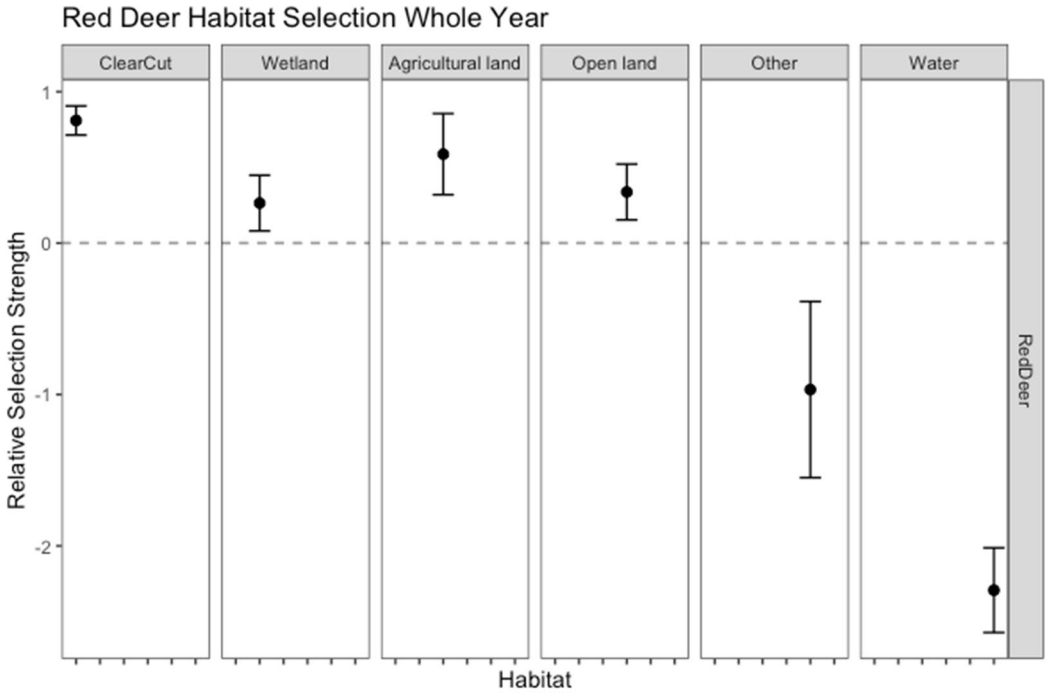

Figure 13. Red deer habitat selection over the full year with habitat forest as response variable (0).

Appendix 3

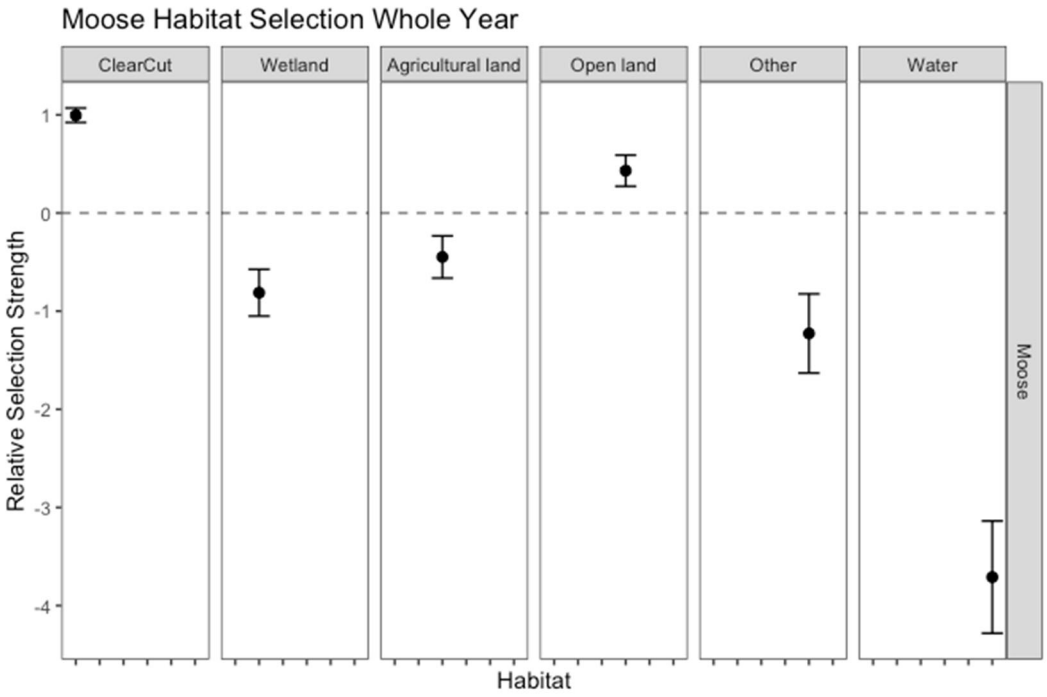

Figure 14. Moose habitat selection over the full year with habitat forest as response variable (0).

Appendix 4

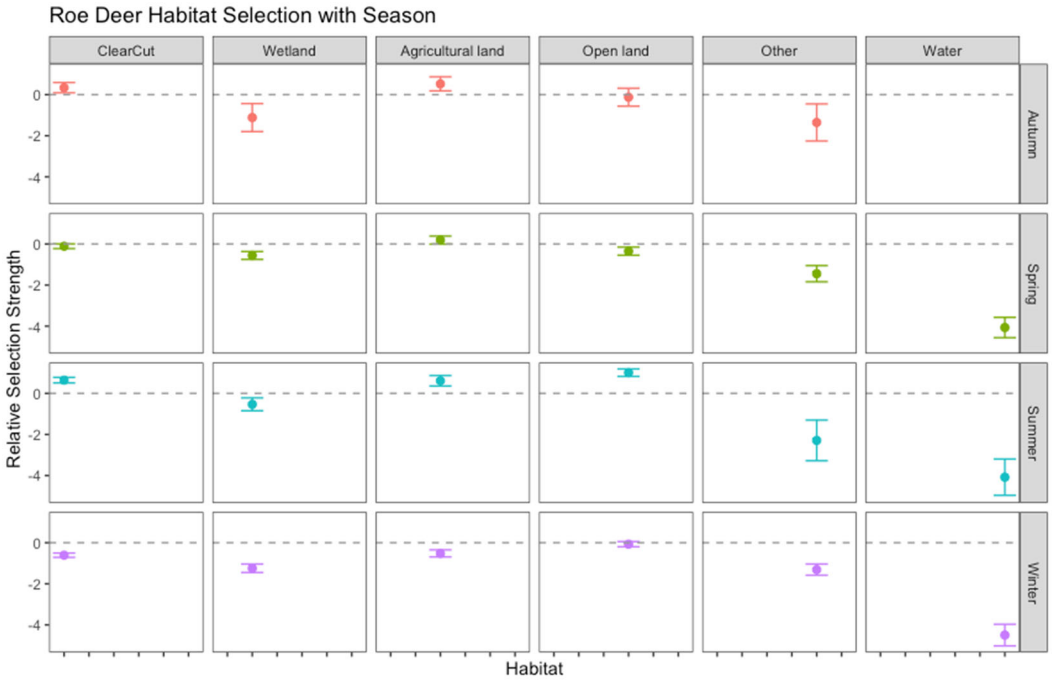

Figure 15.Roe deer habitat selection in response to season of the year with habitat forest as response variable (0).

Appendix 5

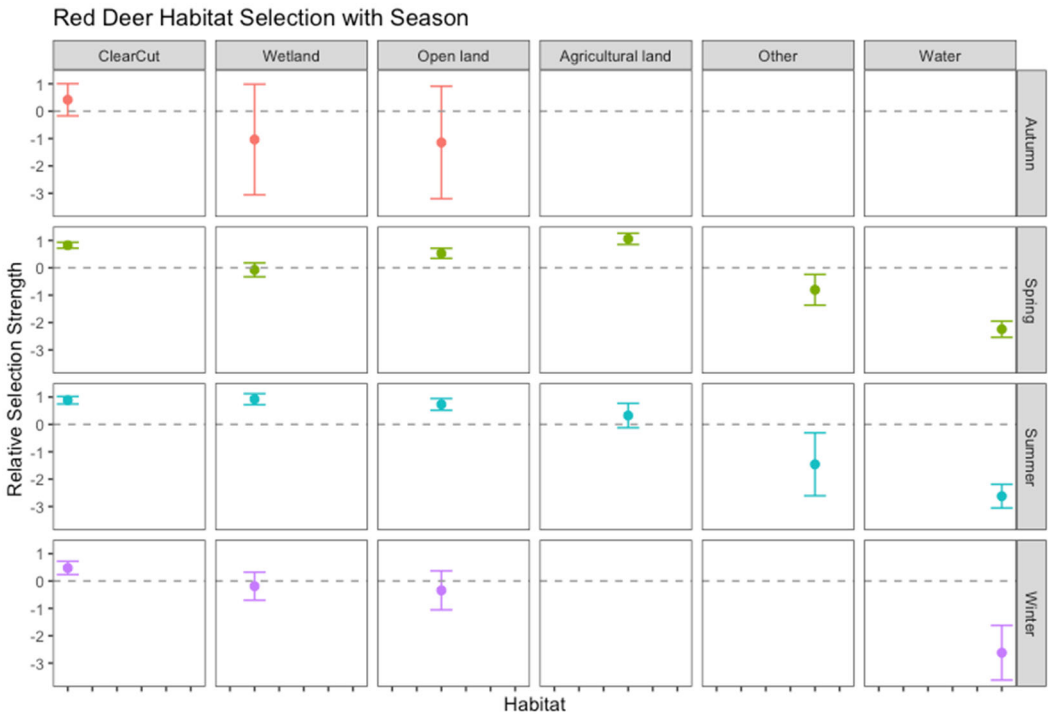

Figure 16. Red deer habitat selection in response to season of the year with habitat forest as response variable (0).

Appendix 6

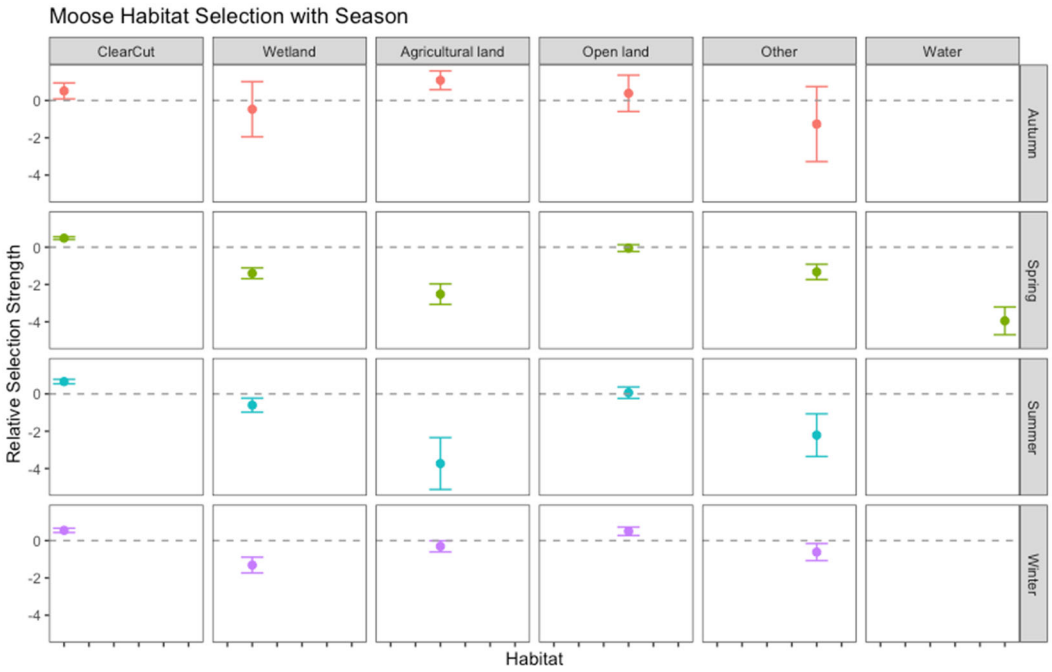

Figure 17. Moose habitat selection in response to season of the year with habitat forest as response variable (0).

Appendix 7

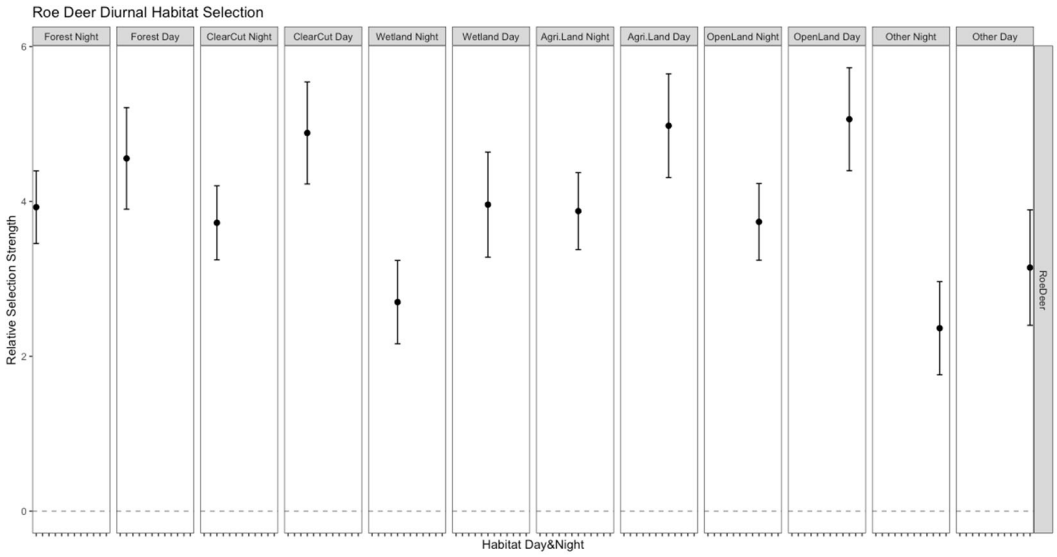

Figure 18. Roe deer diurnal habitat selection.

Appendix 8

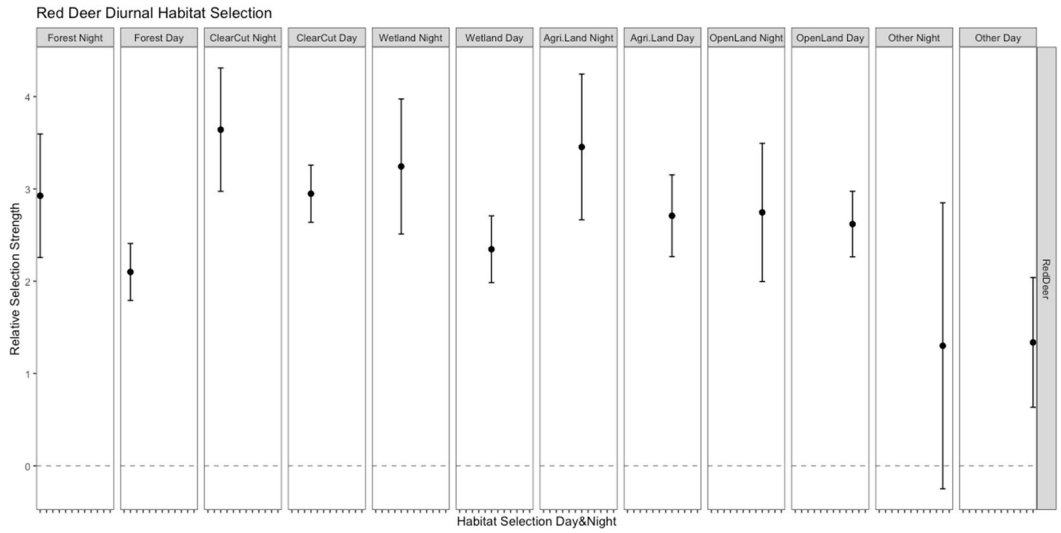

Figure 19. Red deer diurnal habitat selection.

Appendix 9

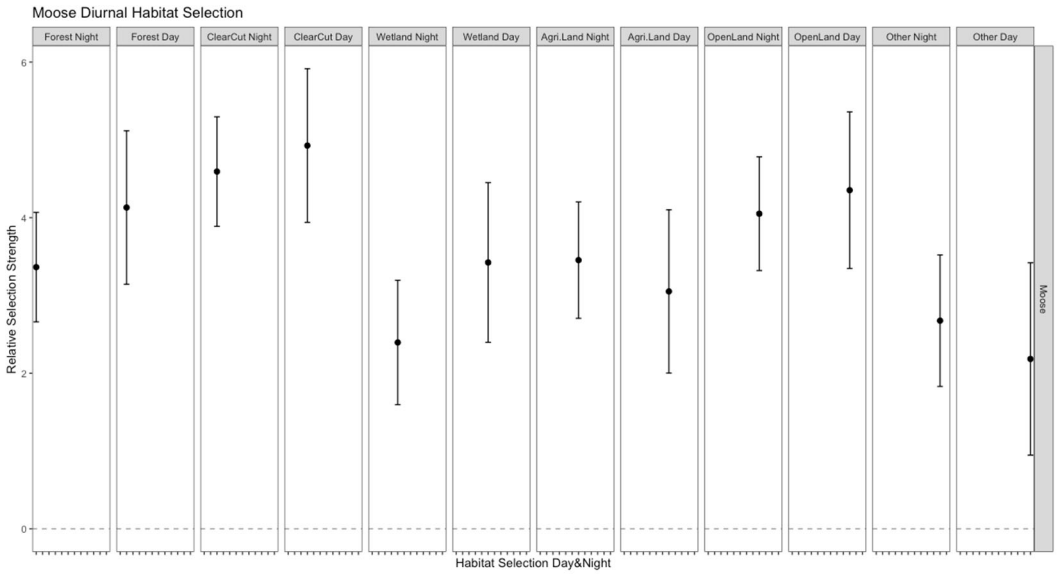

Figure 20. Moose diurnal habitat selection.

Appendix 10

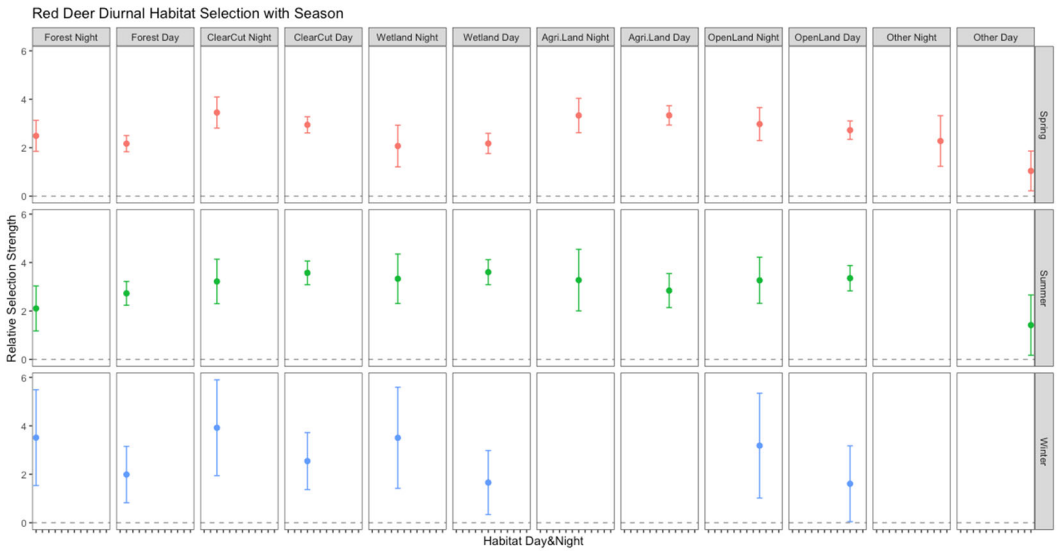

Figure 21. Roe deer diurnal habitat selection in response to season of the year.

Appendix 11

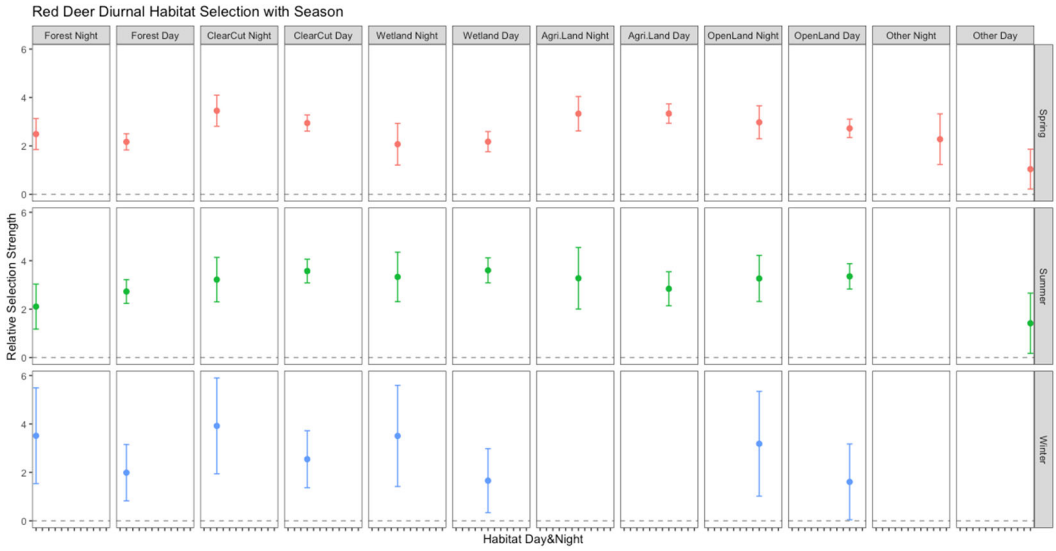

Figure 22. Red deer diurnal habitat selection in response to season of the year.

Appendix 12

Figure 23. Moose diurnal habitat selection in response to season of the year.

Appendix 13

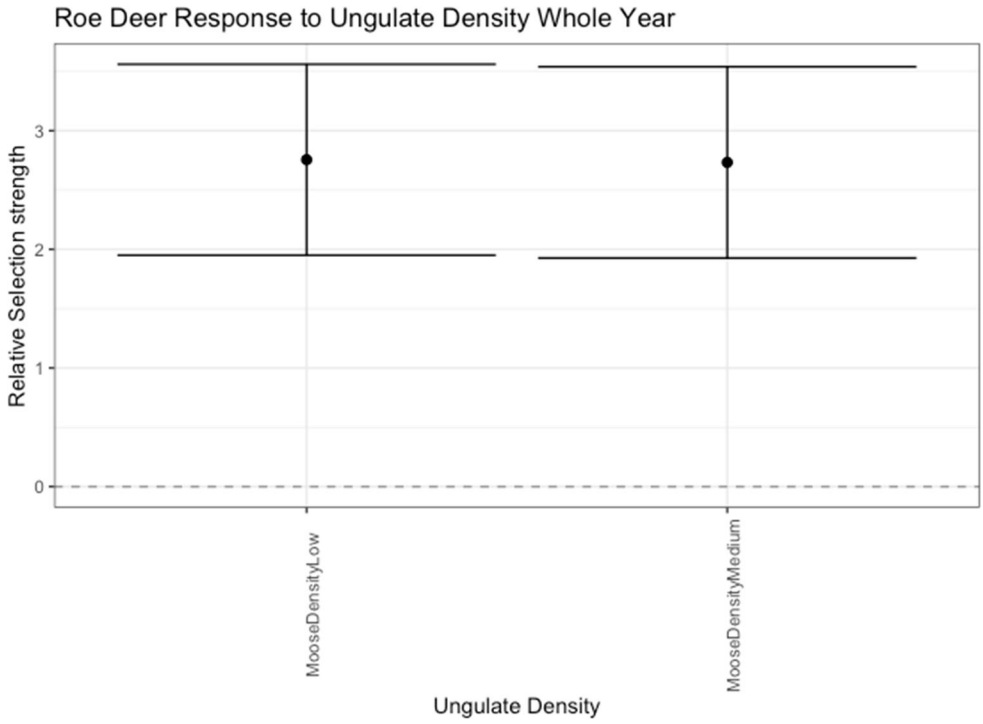

Figure 24. Roe deer response to ungulate densities over the full year with high density as response variable.

Appendix 14

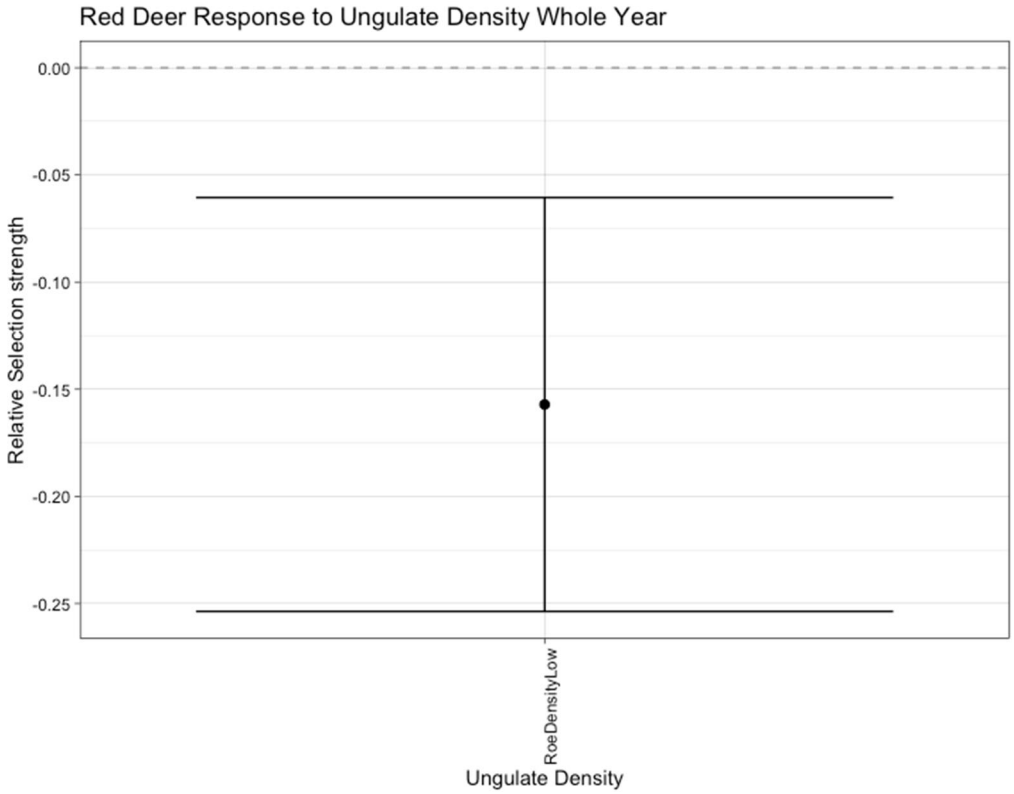

Figure 25. Red deer response to ungulate density over the full year with high density as response variable.

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